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Diverging distribution of seedlings and mature trees reflects recent climate change in British Columbia

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ABSTRACT

The composition and health of forests across western North America have shown signs of change over the last half-century associated with altered climate conditions. Most models developed to predict responses to variation in climate assume that the ecological distribution of adult trees provides a sound basis for projecting potential shifts in a species' range. Under a dynamic climate, however, recently established seedlings may more closely reflect changes in climate conditions. This study combined the simple, widely tested physiological model 3-PG with an empirical regeneration dataset, composed of 21,097 plots, to assess regional scale changes in tree species distributions across British Columbia, Canada. We geographically registered all plot locations to correspond with topographically-adjusted 1 km monthly climatic data for the period 2000–2009. By comparing the distribution of seedlings to that of mature trees present in an earlier period (1950–1975), we could assess where alterations in the environment have occurred, and the extent to which changes may make a species vulnerable to replacement in some places or likely to regenerate and migrate elsewhere. Decision tree models were developed to assess the relative importance of suboptimal temperatures, frost, soil water deficits and evaporative demand on the growth and distribution of four widely distributed species: Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), and subalpine fir (*Abies lasiocarpa*). Tree responses varied by species, with areas suitable for lodgepole pine experiencing the largest relative increase in summer drought and areas dominated by western larch experiencing the least. Those areas modelled as suitable for species range expansions occurred 79% (SD = 16%) of the time in places where seedlings of a designated species were predicted in 2000–2009 using the regeneration dataset. We conclude that employing seedling surveys in concert with tree surveys provide valuable ecological insights when predicting species responses to climate shifts.

1. Introduction

Forest ecosystems provide many important ecological benefits, including habitat for wildlife and a continued source of clean water and air (Bonan, 2008; Spittlehouse, 2008). Many local communities depend on forests for timber as well as for their cultural and spiritual values (Millennium Ecosystem Assessment, 2005). Maintaining these ecosystem services requires an improved understanding of how forests are responding to a changing climate.

Increases in disturbances caused by insect attacks (Raffa et al., 2008; Anderegg et al., 2015), diseases (Ramsfield et al., 2016; Woods et al., 2010), and wildfires (Westerling et al., 2006) are associated with climatic variation over recent decades (IPCC, 2014). Small changes in temperature and precipitation impact seedlings more than adult trees, whereas the opposite is the case with bark beetles and wind storms. The life stage of a species individual matters in predicting the future composition of a forest (Bose et al., 2016; Bell et al., 2014; Niinemets, 2010).

In some parts of a species' range, a shift in climate may induce stress, while elsewhere conditions may improve, fostering range expansion (Mathys et al., 2017; Coops et al., 2011; Rehfeldt et al., 2014; Gray and Hamann, 2013). Most species distribution modelling efforts attempt to include a large part, if not all, of a species' natural range. In doing this, there is an underlying assumption that the climatic envelope encompassing the species' range represents those niches where a species is able to survive in the presence of the existing complement of organisms. This complement includes not only other tree species but biological agents that limit tree growth and survival, including native

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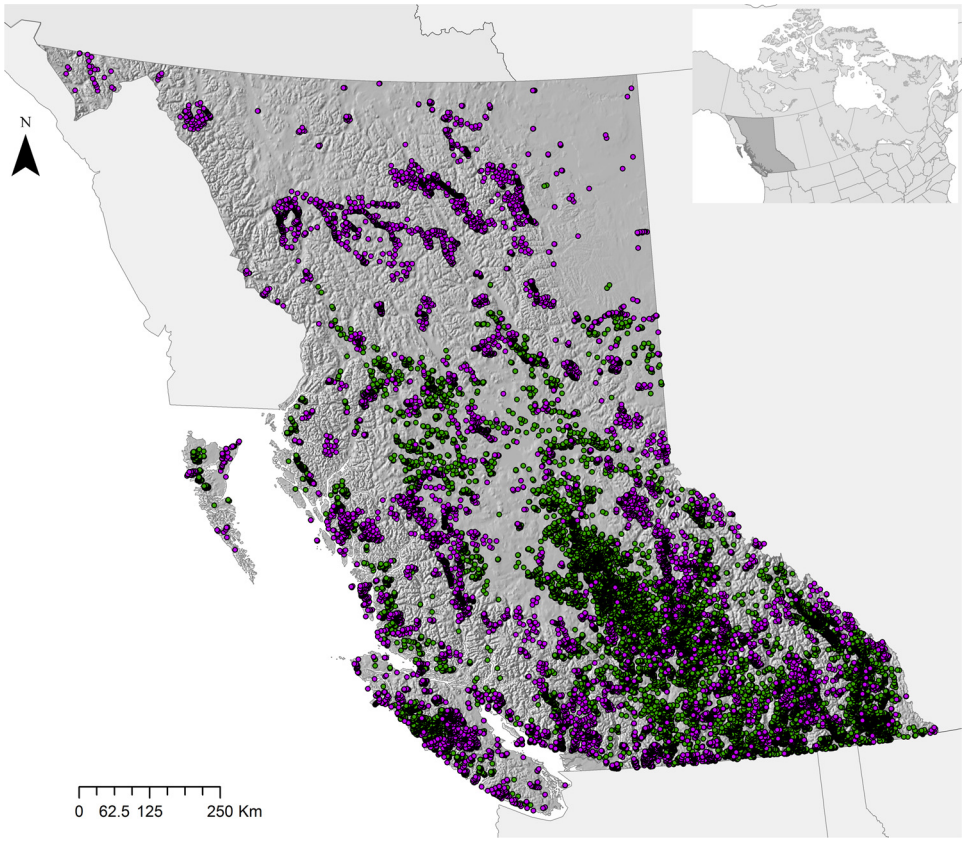

Fig. 1. Location of the survey plots of mature trees (purple) and seedlings (green) in British Columbia (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.).

and introduced herbivores and pathogens. Climate change may reduce niche space, not necessarily because a species might not grow as well, but because previously benign relationships become lethal.

The response of different tree species to climate can be characterized by quantifying relationships between species occurrence and environmental variables (Guisan and Thuiller, 2005). Data mining approaches such as random forest algorithms have also been employed, first to accurately assess current patterns of a species' distribution and then to demarcate probable future habitat (Rehfeldt et al., 2014; Iverson et al., 2008). For example, Gray and Hamann (2013) used a climate-envelope model with random forest algorithm to map the potential future distribution of major tree species in western North America. Coops et al. (2009) introduced a hybrid modelling approach that compared the environmental sensitivities of different western tree species with those predicted using a process-based model parameterized for a single, widely-distributed conifer (*Pseudotsuga menziesii*). An alternative approach, based on the observed growth of different populations observed in common garden experiments, has been used to predict responses to assisted migration of different genotypes under a changing climate (Wang et al., 2010; O'Neill et al., 2008). Unfortunately, data requirements for genetics-based models limit the approach to a few widely studied species (Aitken and Bemmels, 2016).

Although the majority of biologically-based climate-response models rely on species occurrence data acquired for mature trees, Nitschke and Innes (2008) provide a notable exception by modelling species' responses within their regeneration niche. We believe that a modelling approach based on the distribution of tree seedlings has merit because the fate of seedlings at the front or rear margin of a species distribution is a more sensitive harbinger of the future than the response of mature trees (Malcolm et al., 2002; Bell et al., 2014; Bose et al., 2016). By incorporating tree seedlings in species distribution models, we gain insights as to how climatic variation affects reproductive success in both previously established and newly occupied niches (Bose et al., 2016). To date, the paucity of seedling data has limited our ability both to assess and model the effects of climate change on forest composition at large spatial scales (Blanco et al., 2009; Weiskittel et al., 2011; Parmesan et al., 2011).

In this study, we took advantage of databases available both on seedlings and established trees. Using a hybrid model developed by Coops et al. (2009), we combined these geographically-registered datasets with physiologically-defined climatic variables to run decision tree models for both seedlings and mature trees of four widely-distributed species in British Columbia (BC). This hybrid model allowed us to combine process-based modeling with sophisticated machine learning algorithms by relating species occurrences with the relative importance of four environmental limitations on photosynthesis rather than simply employing climatic data.

In an earlier study, Mathys et al. (2014) mapped the baseline distribution of native tree species using climate and soil information with an average accuracy of 84%. The objective of this study was to refine these models to evaluate the extent that predicted tree species shifts were in agreement with seedling observations of four species. We focused the area analysed on BC and selected interior and coastal Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco var. *glauca* (Beissn.) Franco and *Pseudotsuga menziesii* (Mirb.) Franco var. *menziesii*, lodgepole pine (*Pinus contorta* (Dougl.)), western larch (*Larix occidentalis* (Nutt)), and subalpine fir (*Abies lasiocarpa* (Hook.)) for the analysis. Finally, we inferred changes in environmental constraints on species distributions over the past decade compared to baseline conditions (1950–1975).

2. Methods

2.1. Study area

Our study area included all forested areas in British Columbia, the most biologically diverse province in Canada (Fig. 1). The province contains distinct ecosystems ranging from coastal forests to alpine tundra (Meidinger and Pojar, 1991). It is part of the Pacific Northwest region, extending south from the Yukon and Northwest Territories across British Columbia. The region encompasses terrains ranging from the Coast Mountains and Southern Rockies to the Interior Plateau and Great Plains (Valentine et al., 1978). The maritime influence of the Pacific Ocean combined with orographic effects of inland mountain ranges accounts for the diverse climate and precipitation patterns recorded throughout the study area (Meidinger and Pojar, 1991). The Coast Mountains cast a rain shadow leading to arid conditions in the south-central Interior of BC. Vegetation throughout the province predominantly comprises coniferous forest.

To make comparisons between seedling and tree life stages across the study area, we selected species with wide distributions and different ranges including those with a high economic and ecological value. Below, we provide some ecological information on the four species selected for analysis.

The coastal variety of Douglas-fir is distributed within the Marine West Coast Forest ecoregion, representing the densest and most productive ecoregion in BC (Klinka et al., 1999). The interior variety of Douglas-fir occurs in montane forests within the Northwest Forested Mountains, including the Thompson-Okanagan Plateau, where it is often associated with an understory of grass. At higher elevations, Interior Douglas-fir occurs in mixed forests, including those dominated by lodgepole pine or western larch.

Lodgepole pine grows in montane and subalpine forests throughout the Northwest Forested Mountains in BC. It is the most widely distributed tree species in BC and a major source of timber (Klinka et al., 1999). Lodgepole pine is a pioneer species that regenerates in even-aged stands following fire, and it occurs less frequently in southern BC with western larch.

Western larch is present in montane forests of southeastern BC on the Thompson-Okanagan Plateau and in the Columbia Mountains. It generally grows in mixed-species stands and is nearly absent on very moist sites (Klinka et al., 1999). This deciduous conifer is of high ecological and economic value and considered the most productive species of the *Larix* genus in North America (Rehfeldt and Jaquish, 2010).

Subalpine fir is largely restricted to high-elevation forests where winter snowpack accumulates throughout the Northwestern Forested Mountain ecoregion in BC. It occurs in continental climates and is nearly absent in warmer and drier climates (Klinka et al., 1999).

2.2. Sampling species distributions

Species occurrence data were obtained for mature trees, defined as well-established sapling and pole-sized trees (dbh > 1.3 cm), as well as for seedlings, which were defined as individuals < 1.3 m in height. The presence and absence of tree seedlings were acquired from the comprehensive RESULTS (Reporting Silviculture Updates and Land Status Tracking System) database provided by the B.C. Ministry of Forests, Lands and Natural Resource Operations (2014). Seedling data were collected from forest openings caused by natural disturbance and forest harvesting and include both natural regeneration and planted species. A total of 21,097 seedling plot locations were mapped from centroids of polygons over forest openings with an accuracy of about 500 m.

Similar information on the presence or absence of adult trees of focal species were obtained for 8909 locations from centroids of stand-level polygons acquired from protected forested areas and using a three-phase, photo- and ground-based sampling design across all forested land in BC (Schroeder et al., 2010). The accuracy of tree plot locations was approximately ± 500 m. Distributions of the survey plots for trees and seedlings are presented in Fig. 1.

2.3. Climate and soil data

Climatic data required for modelling included monthly mean air temperature, precipitation, evaporative demand, the frequency of frost and solar radiation. The datasets were compiled at a spatial resolution of 1 km. Monthly maximum and minimum air temperature and total precipitation were acquired from ClimateWNA, which downscales 2.5 gridded arcmin PRISM (Parameter-elevation Regressions on Independent Slopes Model) data (Wang et al., 2016; Daly et al., 2008). The climate data were refined to accommodate steep transitions in mountainous areas by adjusting temperature values of heterogeneous terrain based on longitude, latitude and elevation using a dynamic local regression function (Wang et al., 2016). We generated elevation data by resampling a 90 m Digital Elevation Model (DEM) obtained from the Shuttle Radar Topography Mission (SRTM) to the desired resolution of 1 km. To obtain vapour pressure deficit (VPD) values, we first calculated maximum VPD as the difference between saturated vapour pressure at minimum and maximum temperatures. The average monthly daytime VPD was then derived as two-thirds of maximum VPD, to obtain a mean daytime value rather than one based on daily extremes (Waring, 2000). The number of days per month with subfreezing temperatures ($\leq 2\,^{\circ}C$) was calculated from empirical equations with mean minimum temperature (Coops et al., 1998). Monthly total incoming shortwave radiation was acquired by combining synoptic and topographic variations obtained from published data sources (Hember et al., 2017; Fu and Rich, 2002; Schroeder et al., 2009).

Soil properties required for modelling included available soil water-holding capacity and soil fertility. Soil maps depicting the spatial variation of these properties were derived at 1-km resolution by taking advantage of the link between soils, climate and forest productivity. Accordingly, Coops et al. (2012) estimated soil properties through model inversion and optimization techniques by adjusting maximum leaf area index (LAI_{max}) values to correspond with those detected by MODIS satellite imagery. Available soil water was allowed to vary from 0 to 300 mm, whereas soil fertility was ranked from 0, representing the poorest soils, to 1, for the most fertile soils (Landsberg and Waring, 1997). In areas where $LAI_{max} < 3.0$, it was assumed that available soil water was more limiting than fertility, an assumption previously confirmed with field observations by Runyon et al. (1994). Soil fertility increased in importance on sites where $LAI_{max} > 3.0$. Accounting for regional variations in soil properties has shown to improve model predictions of the distribution of tree species (Mathys et al., 2014).

2.4. Modelling tree and seedling distributions

We used a hybrid approach to model tree and seedling distributions that combined a process-based model with automated decision tree analysis (Fig. 2, Coops et al., 2009). The first step involved employing physiological principles to model the environmental constraints imposed on a reference species that affect its current distribution. The second step involved running decision tree analysis for each species to determine how different combinations of environmental limitations define their distribution. The hybrid model was run separately for trees and seedlings to produce species distributions over different time periods.

There are a variety of physiologically-based process models, but only few have been designed to scale projections of photosynthesis, structural growth and mortality across landscapes (Nightingale et al., 2004). Among the most widely used is the Physiological Principles Predicting Growth (3-PG) model (Landsberg and Waring, 1997). The 3-PG model differs from others primarily in a number of simplifying assumptions: (1) that monthly mean climatic data are adequate to capture seasonal trends in growth; (2) that autotrophic respiration (R_a) and net

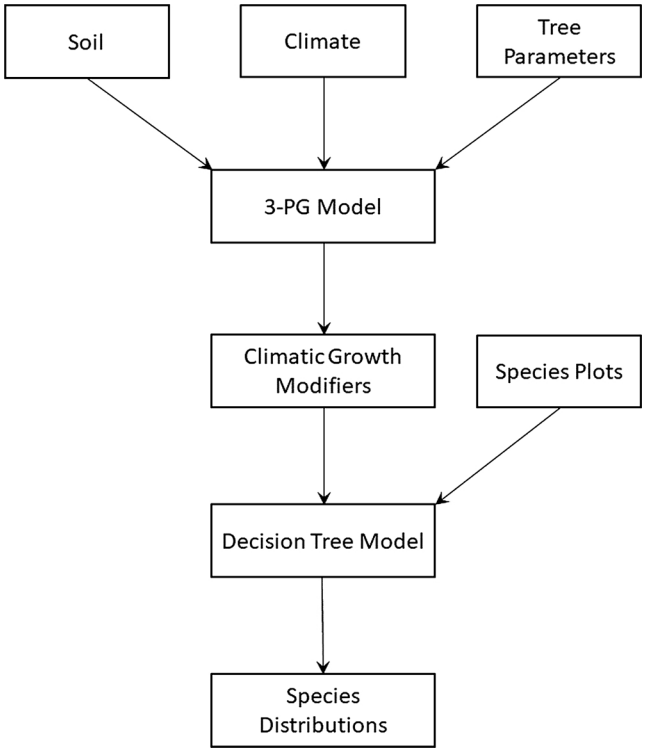

Fig. 2. Flow chart of hybrid modelling approach to simulate tree species distributions. The process-based model 3-PG is first employed by using soil, climate data and tree growth parameters as inputs. The resulting climatic growth modifiers are then combined with tree species plots using automated decision tree analysis.

primary production (NPP) are approximately equal fractions of gross photosynthesis (GPP); and (3) that the proportion of NPP allocated to roots decreases linearly from 60% to ~25% as nutrients, particularly nitrogen, become more available (Landsberg and Sands, 2011).

The 3-PG model calculates gross photosynthesis, canopy evaporation and transpiration, growth allocation and litter production at monthly intervals. It reduces potential photosynthesis and transpiration by imposing restrictions on stomatal conductance through modifiers as defined above between 0 and 1 for suboptimal temperatures, frost, high daytime evaporative demand, and drought as imposed by a soil water deficit (Landsberg and Waring, 1997).

The soil water modifier is determined as a non-linear function of the ratio of the amount of water available in the root zone compared to the maximum value, which is the difference between the water content at field capacity and that at wilting point. The available water content is calculated from knowledge of the previous month's water storage, less the amount of the current month's precipitation minus evaporation and transpiration. Any excess water beyond field capacity drains below the rooting zone or runs off the surface. Transpiration is calculated from the Penman–Monteith equation, which incorporates a canopy conductance term derived from stomatal conductance and LAI (Landsberg and Waring, 1997; Monteith, 1965).

Outputs of the 3-PG model include environmental constraints on species growth such as mean monthly values of air temperature, frequency of frost, soil water and daytime VPD. These were normalized by assuming a continuous scale between 0 and 1, where factors causing no limitations received a value of 1, while those preventing photosynthesis received a value of 0. We then averaged the monthly climatic growth modifiers seasonally and annually for modelling purposes. We chose Douglas-fir as our reference species to parameterize the 3-PG model. Ideally, the parameterization would be carried out for each species individually, however the comprehensive data required for this task is only available for the most widely studied species. Instead, the relative importance of environmental constraints on other species was described, using decision tree analysis, in terms of how their tolerances deviated from optimal conditions of Douglas-fir.

Decision tree models were developed by combining presence and absence data recorded in surveys with corresponding geographically registered climatic data. Decision tree models defined areas where a species appeared to be well adapted as well as where it approached its ecological limits (Coops et al., 2009; Coops et al., 2011). To construct decision tree models, we first extracted seasonal averages of climate modifiers at each of the plots where a species was recorded. The relative importance of each of the seasonal environmental variables was then ranked using Decision Tree Regression software (DTREG, Sherrod, 2010) to predict the presence and absence of each tree species across the region. We built separate decision tree models for each set of survey data. For mature trees, we used the climate growth modifiers produced from a decision tree analysis using monthly averaged climate data from 1950 to 1975, whereas for seedlings, we used a more recent warmer and drier period from 2000 to 2009 (Waring et al., 2014). Model accuracies (Table 1) were evaluated using a 10-fold cross-validation technique (Breiman et al., 1984) and a Kappa statistic (κ).

We predicted the potential expansion or contraction of each tree species' range with 2000–2009 climatic data, using decision tree analyses established under baseline conditions in the 1950–1975 period. If the probability of a tree species' occurrence was ≥70% in 2000–2009, while under baseline conditions it was predicted to be absent, we designated such areas as suitable for species expansion. Alternatively, species in areas where the environment was predicted to be no longer favourable for a species 70% of the years since 2000 were considered vulnerable to replacement by other species (Mathys et al., 2017).

The potential for range expansion under a rapidly changing climate is often much larger than can be attained, at least without assisted migration. In recognition of this fact we set a limit of 200 m as the maximum distance a population of a tree species can migrate annually. This value was derived from information in the paleoecological records (Mathys et al., 2017, Davis,1989; Beckage et al., 2008). Finally, we used the decision tree models developed for seedlings in 2000–2009 to assess the extent of agreement with decision tree models based on tree data acquired in 1950–1975 and projected to the period of 2000–2009 to identify areas of likely range expansion and contraction. In this paper we did not attempt to predict the location of disturbances in response to variation in climate (but see Waring et al., 2011, Waring and Coops, 2016).

Table 1
Accuracies of decision tree models in predicting the occurrence of tree species in BC over the period of 1950–1975 and of seedlings during 2000–2009. Brackets represent 95% confidence intervals.

Species	Presence accuracy (%)		Overall accuracy (%)		κ	
	Tree	Seedling	Tree	Seedling	Tree	Seedling
Subalpine fir	90 (± 2.0)	81 (± 1.1)	62 (± 1.0)	72 (± 0.6)	0.8147	0.6634
Douglas fir	78 (± 1.6)	91 (± 0.5)	72 (± 0.9)	75 (± 0.6)	0.615	0.7079
Western larch	94 (± 3.4)	86 (± 1.2)	83 (± 0.8)	69 (± 0.6)	0.9299	0.7631
Lodgepole pine	78 (± 1.7)	79 (± 0.8)	61 (± 1.0)	67 (± 0.6)	0.515	0.4398

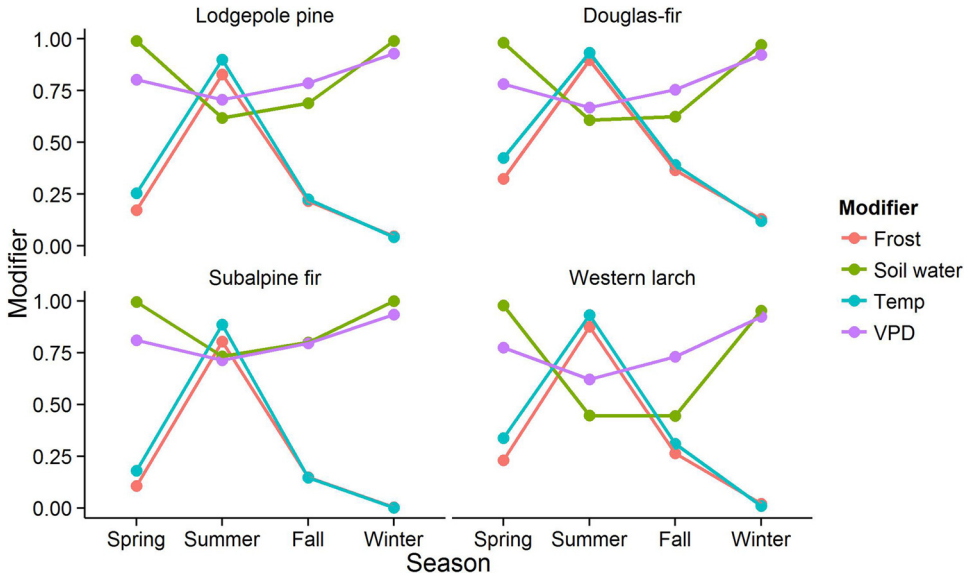

Fig. 3. Mean seasonal variation in climatic growth modifiers for the mature trees: lodgepole pine, Douglas-fir, subalpine fir and western larch during the baseline period from 1950 to 1975 (0 = no growth and 1 = optimum conditions for growth).

3. Results

3.1. Changes to climatic growth modifiers

The importance of the assessed seasonal climatic modifiers, averaged across all plots, differed among species during the baseline period 1950–1975 (Fig. 3). Both Douglas-fir and lodgepole pine were limited mainly by suboptimal air temperature and frost in winter when these modifiers restricted growth by over 85%. Growth of these two species was not severally limited by soil water deficits (38%–39%) or evaporative demand (29%–33%) in summer. On sites occupied by Douglas-fir, growth was also constrained by suboptimal temperatures and frost occurrence in spring and fall, but the major limitations were imposed in winter. The growth of subalpine fir in higher-elevation forests was severely restricted (> 82%) by low temperatures in spring and fall. Limitations from drought and high evaporative demand caused < 30% restrictions on subalpine fir growth during baseline conditions. In contrast, western larch experienced soil water deficits during summer in southeastern BC that limited photosynthesis by up to 55%, while frost imposed > 20% reductions in growth in spring and fall.

Comparison of the two time periods (1950–1975 and 2000–2009) showed that the greatest mean differences of the seasonal modifiers occurred predominantly in spring and summer at the surveyed plots (Fig. 4). Tree seedlings have been exposed to increased summer soil water deficits under recent climate conditions than mature trees were during the earlier period (1950–1975). Summer VPD also showed some decreases in 2000–2009 compared to baseline conditions. Springtime temperatures and frost became less limiting between these periods, although on average they remained the most constraining environmental factors.

At the species level, both lodgepole pine and subalpine fir had the greatest shift in mean seasonal modifier values, suggesting weaker constraints from unfavourable spring temperature and frost but increased limitations by drought and vapour pressure deficits in 2000–2009 compared to 1950–1975 (Fig. 5). Areas favourable for these two species registered the largest relative increase from the effect of drought in summer, whereas those areas dominated by western larch experienced the least. All species experienced a rise in spring temperatures across their current ranges, and these were most pronounced for subalpine fir and lodgepole pine, and least pronounced for Douglas-fir. In contrast, summer vapor pressure deficits increased the most in

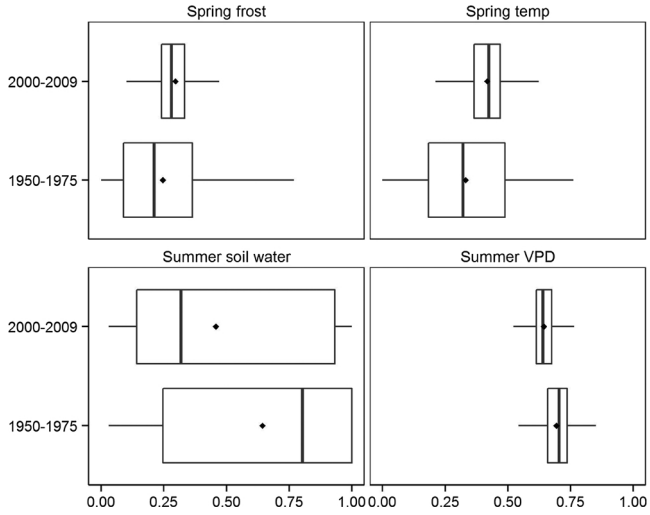

Fig. 4. Shifts in mean (dots), median (line) and interquartile range (box) between the two periods (1950-75 and 2000-09) for the seasonally-defined climatic growth modifiers: spring frost, spring temperature (temp), summer soil water and summer vapour pressure deficit (VPD).

areas occupied by lodgepole pine and least in areas favourable for western larch. With regard to limitations by spring frost, conditions improved the most for subalpine fir and changed the least for Douglas-fir. Environmental conditions in BC are improving for Douglas-fir as soils become drier and frost less frequent during the active growing season.

3.2. Species vulnerability assessment

Vulnerability of tree species to a changing climate in 2000–2009 compared to baseline conditions is shown in Fig. 6, illustrating climatically-suitable areas for species expansion as well as where a species is predicted to encounter increased stress. Lodgepole pine was predicted to become increasingly stressed throughout its historic range in the Interior of BC with changing climate conditions (Fig. 6a). Approximately 4% of its baseline distribution was classified as no longer suitable with some areas (1%) becoming climatically suitable for range expansion (Table 2). Western larch displayed the greatest potential for

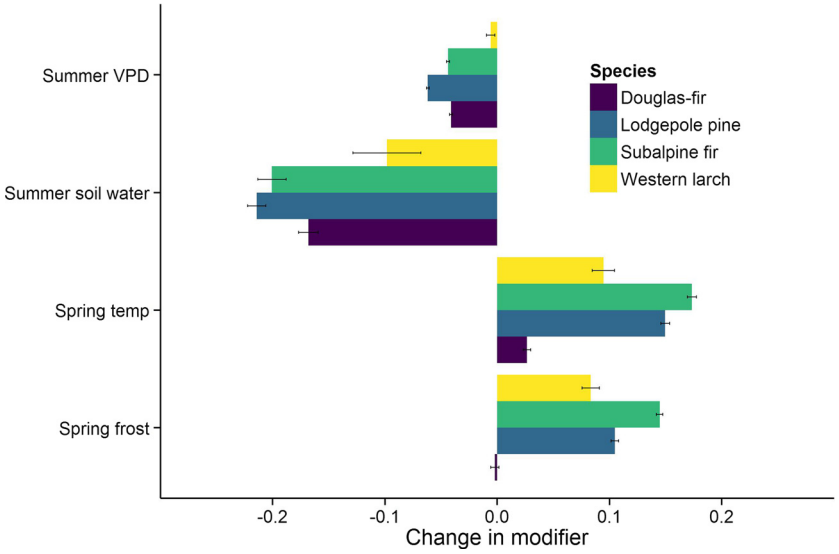

Fig. 5. Changes in seasonal climate growth modifiers for Douglas-fir, lodgepole pine, subalpine fir and western larch between 1950–1975 and 2000–2009. The error bars represent the standard error. Positive values indicate that a modifier is becoming less limiting.

range expansion (10%) of the four species analyzed in this study (Fig. 6b; Table 2). Western larch was projected to expand northwest from its historic range in Interior BC and displayed only limited stress under recent climate conditions.

To assess model performance, we compared the areas of predicted species range expansions and contractions with habitat favourable for seedlings (Table 2; Fig. 6). In general, there was good agreement between areas where trees were projected to expand or contract their range and the observed distribution of tree seedlings as simulated based on records in the RESULTS database. The areas deemed suitable for expansion agreed 79% on average with successful seedling establishment and areas classified as stressed had an average agreement of 77% with areas where the seedlings were absent.

4. Discussion

In this study, we applied an approach that identifies emerging shifts in the distribution of species by comparing the observed distributions and potential growth responses of two life stages: seedlings and trees. Information on seedling occurrences obtained from the regeneration database served as a sensitive, early indicator of tree responses to climate change. Estimates of species vulnerabilities from this study agreed well in most cases with observed seedling establishment (Table 2). The distribution of subalpine fir seedlings displayed the lowest agreement with areas we predicted as stressed. The lower number of tree plots compared with those for seedlings may have led to a higher accuracy of the regeneration predictions (Table 2). In any case, our analysis suggests that the projected stress at these sites is not yet sufficiently severe to induce mortality of the species. In general, differences in the distribution and climate exposures of seedlings compared to those of trees established last century provided evidence that some species expansions have already occurred in response to climate change (Lenoir et al., 2009).

Tree responses to changing environmental limitations during the two periods varied among the four species analysed. Both lodgepole pine and subalpine fir experienced the greatest changes in environmental constraints on sites where they currently occur and also had the most areas classified as stressed in the model predictions. In the past, sites occupied by these species experienced only limited soil water deficits. That situation is now changing, posing increased stress on the species. Although lodgepole pine is a widely distributed species adapted to a range of environments (Klinka et al., 1999), warmer temperatures and reduced frost can create an environment for both competing species and damaging biotic agents to thrive. In recent years, lodgepole pine forests have been exposed to increased bark beetle attack and diseases that have affected forest health and may limit their habitat in the future (Monserud et al., 2008, McKenney et al.,2007; Mathys et al., 2017, Carroll et al.,2006; Mather et al., 2010). In contrast, the two temperate species, Douglas-fir and western larch, both displayed the opportunity and capacity to expand northward as changing environmental conditions, such as increasing air temperatures and reduced snowpack, are likely providing favourable conditions for this species to migrate.

Incorporating a large regeneration dataset together with climate data in physiological modelling provided valuable information on crucial environmental stressors impacting species distribution patterns. Results from this study indicated that warmer temperatures, reduced frost, and increased drought occurred in some places in recent years, causing shifts in forest composition. All species analysed in this study became increasingly limited by soil water deficits, as environmental factors such as low temperatures and frost occurrences became less constraining with climate change. This greater exposure to summer drought will be important to monitor to determine a species' ability to tolerate such changing conditions. Species that are more drought-adapted such as Douglas-fir have a competitive advantage as warming trends continue.

In agreement with this study, the suitable habitat of more southern species such as Douglas-fir and ponderosa pine has been projected to expand northward and upward by Rehfeldt et al., (2014) and Gray and Hamann (2013). These two studies projected an even greater northward expansion of Douglas-fir range within the Northwest Forested Mountains than our study, although at a lower frequency (< 5%) (Gray and Hamann, 2013, Rehfeldt et al.,2014). The suitable habitat of western larch has also been previously predicted to expand northward in BC (Rehfeldt and Jaquish, 2010) and management practices now allow planting small amounts of western larch north and west of its current distribution (Jaquish, 2010). Areas we classified as suitable for western larch expansion agreed well with the mapped guidelines for seed transfers by Rehfeldt and Jaquish (2010), although we also predicted areas further northwest in the Thompson-Okanagan Plateau to become suitable with changing climate conditions.

Empirical studies that have analysed the distribution of trees and seedlings generally report migrations of species toward higher altitudes and latitudes (Woodall et al., 2009, Monleon and Lintz,2015; Lenoir et al., 2009), although caution has been expressed in using the

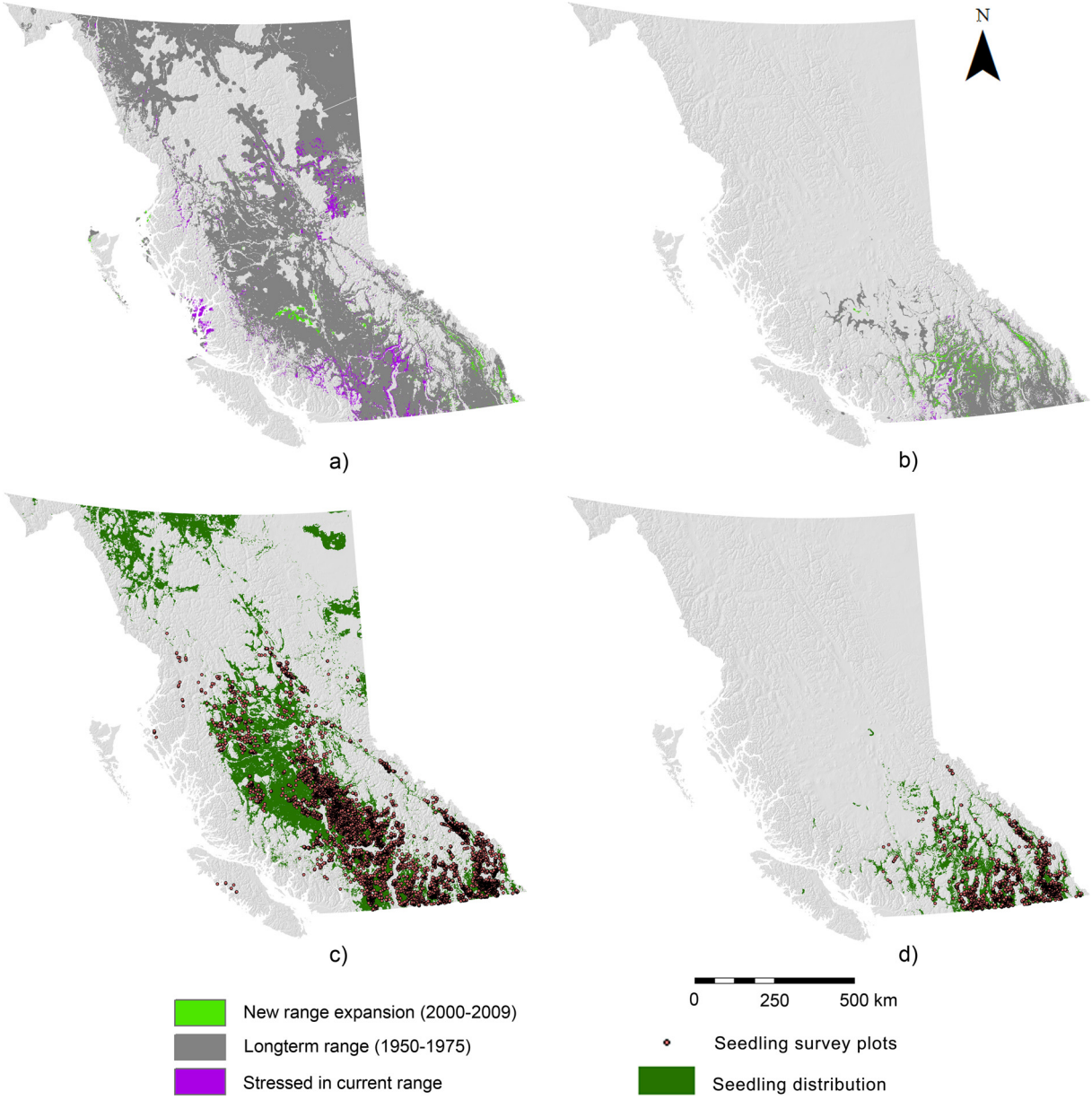

Fig. 6. Potential for range expansion and vulnerability of a) lodgepole pine and b) western larch based on 2000–2009 climatic conditions compared to conditions during 1950–1975 and suitable habitat for seedlings of c) lodgepole pine and d) western larch as predicted from RESULTS.

Table 2
Percent agreement between modelled tree species vulnerabilities and area deemed suitable or unsuitable for regeneration (2000–2009).

Species	Expansion (%)		Stress (%)	
	Projected	Agreement	Projected	Agreement
Douglas-fir	5	92	1	99
Lodgepole pine	1	62	4	82
Western larch	10	67	2	99
Subalpine fir	0	97	16	25
Average	4	79	6	77

distribution of different life stages as evidence of species range shifts (Sittaro et al., 2017). In the dry portions of western US, the distribution of tree seedlings was predicted to decline, especially in subalpine areas (Bell et al., 2014). The effects of climate change are greater at higher altitudes, where tree species are most sensitive to changing conditions (Lenoir et al., 2009, Kullman, 2007). Unlike these empirical studies, our approach allowed us to not only assess divergences in tree and seedling distributions but also to predict changes to the physiologically based stresses that are limiting the species and offer some insights that may modify forest management practices to buffer conditions against rapid change.

It may be simplified to assume that species responses to changing environmental conditions are identical for seedlings and mature trees. Tree seedling distributions are not only affected by growth but also by germination and success in establishment (Blanco et al., 2009), factors that are currently omitted by the 3-PG model. Nonetheless, the tree seedling inventory used in this study reflects the occurrences of those species that had successfully established and survived in their natural environment. The RESULTS database focused on areas that have undergone silvicultural activities for reforestation and that have been planted with seedlings. It would be valuable to also have information available on natural regeneration in BC to compare with model predictions. Still, the current dataset was useful in providing insights on the actual inventory of regeneration in the province as influenced by

forest management practices. Furthermore, seedlings were only planted within current species ranges; thus species shifts, as identified in this study, reflect climatic influences rather than changes in management practices.

Continuous forest monitoring in permanent plots at decadal intervals would improve our models in addition to our understanding of how a progressively changing climate impacts tree mortality and regeneration and thereby forest composition. It is also desirable to seek more representative data on species growth, distribution, and site characteristics. We encourage a multitude of approaches to improve models, including those incorporating interactions with rising atmospheric concentrations of CO_2 (Waring and Gao, 2016) and genetic effects (Wang et al., 2010). Including forest disturbances in species distribution models should improve predictions of stresses that are expected to increase with climate change (Rehfeldt and Jaquish, 2010), for example by incorporating projections of fire occurrences (Waring and Coops, 2016) or outbreaks of insects and pathogens (Woods et al., 2010, Mather et al., 2010). Incorporating a regeneration module within 3-PG would also improve predictions by including microclimatic variation in light and frost (Ribbens and Pacala, 1994; Canham et al., 1994). It would be more challenging to create a model that included the mechanical limitations imposed by browsing, snow and ice (Holmgren et al., 1997). The version of the 3-PG model used in this study is also only applicable for conifer trees. Recently, the model has been modified to account for deciduous and mixed species forests by adjusting for differences in light absorption and within-canopy vertical gradients in climate (Forrester and Tang, 2016). Differentiating soil water access for seedlings versus trees would also refine model predictions, as we highlight the increased importance of drought on species growth. For example, young ponderosa pine trees have been found to be more sensitive to drought earlier in the season compared to older trees (Irvine et al., 2002). Accounting for differences in rooting depth with tree age can contribute to improving predictions of species responses from regeneration to maturity.

This study highlighted how climate shifts are leading to changes in tree species distribution patterns as affected by alterations of the environmental limitations on species growth. Employing an extensive regeneration dataset allowed us to compare and contrast predicted areas suitable for tree species range expansion with those where tree seedlings have been successfully established. While species such as lodgepole pine and subalpine fir likely experienced increased stress with climate change, there was potential for species such as Douglas-fir and western larch to expand their range as survival conditions improved. Knowledge of the crucial stressors on tree species and where to expect potential for species range expansions can be useful for forest managers developing mitigation practices to climate change. The most important contribution of our analysis is perhaps the approach itself, where the distribution of two life stages in a species are compared in reference to their appearance or absence on recorded plots over contrasting periods, representing subtle but progressive shifts in climatic conditions. We hope to see the approach extended and tested more widely in western North America and beyond.

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